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Abstract

Exogenous and endogenous environmental factors can have simultaneous additive as well as interacting effects on life-history traits. Ignoring such interactions can lead to a biased understanding of variability in demographic rates and consequently population dynamics. These interactions have been the focus of decades-long debates on the mechanisms underlying small mammal population fluctuations. They have often been studied indirectly through seasonal effects, but studies considering them directly and more mechanistically are rare. We investigated the joint effects of exogenous (temperature, food availability) and endogenous (population density) factors on the demographic rates of a group-living diurnal rodent, the African striped mouse (*Rhabdomys pumilio*) using nine-year mark-recapture data from a population in the Succulent Karoo, South Africa. In general, higher temperatures and lower food availability were associated with higher survival, whereas high population densities were either beneficial or detrimental to survival depending on interacting food availability. High reproductive rates were related to lower temperatures, higher food availability and lower population density, and interactions among environmental factors mediated the strength of these relationships. Our study highlights the complex ways in which different environmental factors can interact to shape demographic rates and emphasizes the importance of explicitly including interactions among exogenous and endogenous factors into studies of population dynamics.

Introduction

The relative importance of exogenous and endogenous environmental drivers in shaping population dynamics is a key topic in population ecology and has received particular attention in the past decades (e.g. reviewed by Krebs 2013). Exogenous (i.e. population extrinsic) factors, such as climate and resource availability, have been demonstrated to play a key role in the regulation of several animal populations (Batzli 1985, Oksanen et al. 2008), whereas in other studies, endogenous (i.e. population intrinsic) factors, including density-dependent regulatory mechanisms, have been proposed as the main force driving population fluctuations (Krebs 1978, Krebs et al. 2007). Today, there is broad agreement that neither exogenous nor endogenous factors alone are sufficient to explain population dynamics and the demographic variability underlying them (e.g. Krebs 2013). Both have to be studied simultaneously in order to gain a thorough understanding of population dynamics and to develop effective wildlife management strategies (Williams et al. 2001).

As a result of this synthesis, research in the past two decades has focused on investigating simultaneous effects of environmental factors on population dynamics. This was mainly done by either considering additive effects of different, continuous environmental factors, or by looking at the effects of a discrete factor such as season. Here, the latter indirectly incorporates interacting effects of environmental factors (Turchin and Ostfeld 1997, Merrit et al. 2001). Modelling non-linear interactions among continuous factors directly has largely been ignored (Coulson et al. 2001, Crain et al. 2008). More recent studies have now highlighted the importance of including these interactions specifically in ecological research in order to gain a more mechanistic understanding of their effects (de Little et al. 2007, Crain et al. 2008, Griffiths et al. 2015). The interaction of two environmental effects can lead to greater

47 or smaller responses than the sum of the individual effects (Crain et al. 2008),
48 depending on the underlying biological processes, such as competition or energetic
49 trade-offs (Previtali et al. 2010, Griffiths et al. 2015). Ignoring such non-additive
50 effects among exogenous and endogenous environmental drivers can lead to false
51 conclusions about their roles in population regulation (Previtali et al. 2010). Previtali
52 et al. (2010), for example, demonstrated that while there was no individual effect of
53 precipitation on deer mouse (*Permomyscus maniculatus*) survival and reproductive
54 rates, the interactions of precipitation with season and environmental disturbance were
55 very important. They showed that survival at disturbed sites was particularly low
56 during summer, and the negative impact of disturbance on survival and reproduction
57 was mitigated by high precipitation (Previtali et al. 2010). A different study found
58 juvenile survival of elephant seals (*Mirounga leonida*) to decrease with population
59 density when its interaction with climate was ignored, but this relationship
60 disappeared when the interaction was considered, showing that stochastic
61 environmental forcing dwarfed negative density feedbacks in this system (de Little et
62 al. 2007). Consequently, identifying and quantifying interactions is crucial in the
63 study of multifactor hypotheses of population regulation.

64 Small rodents represent suitable model systems for studying multifactor
65 hypotheses on demographic rates variability, including interactions among exogenous
66 and endogenous environmental factors. As fast life history species (*i.e.* shorter life
67 spans and high offspring production with relatively low survival prospect), their
68 individual life-history traits are highly sensitive to changes in both exogenous and
69 endogenous environmental factors. This demographic sensitivity in combination with
70 the wide geographical distribution of rodent species provides a unique opportunity to
71 study the impacts of the same environmental factors interacting at both different time-

72 scales and across habitat types and continents (Krebs 2013). This is highly valuable
73 for generalizing hypotheses about interactive effects among environmental factors.
74 The aim of our study was to assess the interacting effects of exogenous and
75 endogenous environmental factors on demographic rates of the African striped mouse
76 (*Rhabdomys pumilio*) in the Succulent Karoo semi desert of South Africa. In addition
77 to fast life histories, this species lives in arid and unpredictable habitats, providing a
78 high level of environmental variability for many generations within a relatively short
79 time period (Schradin and Hayes, in review). We used nine years (2005-2014) of
80 monthly mark-recapture data to parameterize a multi-state mark recapture model and
81 generalized linear (mixed) models, tested several system-specific hypotheses (detailed
82 below) regarding environment-demography relationships and investigated the role of
83 interacting effects in population regulation.
84 For our analysis, we considered ambient temperature and food availability as
85 exogenous factors, and population density as an endogenous factor. Exogenous
86 factors investigated in multifactor studies frequently include temperature as an
87 important climatic variable (Ferreira et al. 2006, Andreo et al. 2009). Rodents from
88 dry environments are challenged with temperatures well above and below their
89 thermoneutral zone, incurring thermoregulatory costs at both extremes (Haim and
90 Izhaki 1995). As the thermoneutral zone of striped mice is rather high (32 ± 1^{o} C, Haim
91 and Fourie 1980), we hypothesized that particularly cold extremes might have a
92 strong negative impact on their survival and reproduction as a result of high energetic
93 costs. We further expected this detrimental effect of low temperatures to be
94 counterbalanced by interactive effects of high food availability (more energy available
95 for physiological thermoregulation) and high population density (limited heat loss due
96 to huddling at night; Scantlebury et al. 2006). Food availability generally determines

97 the amount of energy available to an animal, and has been found to have a positive
98 influence particularly on rodent reproduction (Dobson and Oli 2001, Pinot et al.
99 2014). We therefore hypothesized that high food availability would result in higher
100 survival and reproductive rates. Among endogenous environmental factors, negative
101 density-dependent feedbacks have been found to be important drivers of rodent
102 population dynamics (reviewed by Krebs 2013). Furthermore, studies found that in
103 habitats similar to that of our study population, population density acted in concert
104 with exogenous factors in shaping demographic rates of rodent species (Leirs et al.
105 1997, Lima et al. 2003). We therefore hypothesized that high population density
106 would decrease survival and reproduction of striped mice, particularly if it acted in
107 concert with low food availability and thus increased intraspecific competition.
108

109 ## Materials and Methods

110 ### Study area

111 This study was conducted in Goegap Nature Reserve in the Succulent Karoo of South
112 Africa (29° 41' 42.5 latitude, 18° 01' 33.4 longitude, 912m altitude). The Succulent
113 Karoo semi-desert is a winter rainfall ecosystem where most of the annual rain
114 (approximately 192±51mm p.a. at our field site) falls between May and September.
115 Vegetation cover is closely linked to rainfall patterns, and therefore has an annual
116 peak in spring, following the winter rainfalls. Ambient temperatures also follow a
117 seasonal pattern, and span a wide range from below 0 degrees Celsius in winter nights
118 to over 40 degrees Celsius during summer days (Supplementary material Appendix 1
119 Fig. A1). Climatic conditions in the Succulent Karoo do not only have strong intra-
120 annual fluctuations, but the amount and timing of rainfall and thus the availability of

121 green vegetation (18.9±8.7 percent ground coverage at the field site) can vary greatly
122 between years (Supplementary material Appendix 1 Fig. A1).
123
124 **Study species**
125 The African striped mouse (*Rhabdomys pumilio*) is a small, diurnal murid rodent
126 (Schradin and Pillay 2004) inhabiting dry regions of southern Africa (Meynard et al.
127 2012). Striped mice form extended family groups with individuals of one group
128 sharing one nest, but foraging solitarily during the day (Schradin and Pillay 2004).
129 The main breeding season coincides with the annual burst of vegetation in the austral
130 spring, usually between July/August and November/December, although reproduction
131 can occur outside this window if sufficient rain falls in summer or autumn. Within the
132 main breeding season, females can have up to three litters of 5.3 pups on average
133 (Schradin and Pillay 2005). Offspring can reach sexual maturity as early as four
134 weeks of age, but most stay with their natal group as philopatric helpers and delay
135 reproduction (and dispersal in males) for several months until the next breeding
136 season (Schradin et al. 2012). Few breeding mice survive to another breeding season,
137 such that striped mice typically breed only during the spring following the breeding
138 season they were born in (Schradin and Pillay 2005).
139
140 **Trapping procedure**
141 The striped mouse population has been monitored using a standard capture-mark-
142 recapture protocol since 2001. Striped mice were trapped using metal live-traps
143 which were placed in front of bushes that were used as nesting sites (revealed by
144 direct observations and radio-tracking). Trapping was done during mornings
145 and evenings, including the time intervals when family groups basked together

146 outside their nests. Trapped mice were sexed, weighed and individually marked
147 with metal ear tags as well as hair dye for individual recognition in the field
148 during observations. During the study period (January 2005 – September 2014), all
149 mouse groups within the study area (19±4 groups on average) were trapped for three
150 consecutive days at least once and typically twice every month. Female striped mice
151 were considered "reproductively active" if a perforated vagina and/or nipples showing
152 signs of lactation were observed. The trapping protocol has been described in detail
153 elsewhere (Schradin and Pillay 2004, 2006). A total of 7745 individuals (2539
154 females and 5206 males) were caught and marked during the 117 trapping sessions
155 within the study period. In our analyses of individual capture histories, we only
156 considered the 1609 female striped mice whose date of birth had been estimated based
157 on their body mass at a young age (method described in Schradin et al. 2009). Data
158 available from the Dryad Digital Repository: hyperlink to be provided (Nater et al.
159 2016).
160
161 **Environmental factors**
162 Our analysis considered three different environmental factors that are hypothesized to
163 play an important role for our study species. They included (1) temperature and (2)
164 food availability as exogenous factors, and (3) population density as an endogenous
165 factor. All environmental factors were analysed on a monthly scale.
166 Mean monthly temperature was calculated by averaging daily minimum and
167 maximum ambient temperatures (measured at the field station, 5cm above ground) for
168 each month. Food availability was estimated as the percentage of ground covered with
169 succulents and ephemerals known to be edible by striped mice (34 species, Schradin
170 and Pillay 2006). To calculate a study site mean of plant cover, we used data from

171 plant surveys conducted on the 15th of each month and averaged the estimates from 8
172 different 2x2m monitoring plots within the study area that were sampled following a
173 standard protocol (Braun-Blanquet method, Werger 1974).
174 We calculated population density by dividing the total number of trapped adult mice
175 of both sexes by the study area. Immature individuals were excluded from the
176 calculations as they do not yet consume much vegetation, forage only very close to
177 their nest (limiting competition with individuals from other groups) and do not
178 partake in reproductive competition. We also included individuals of unknown age in
179 the density calculations, and therefore defined the immature stage for individuals
180 below 20g of weight here (based on a mass-at-age regression, Schradin et al. 2009).
181 This definition of the immature stage using weight overlaps strongly with the
182 definition based on age (Supplementary material Appendix 2 Figure A2). Trapping
183 directly at the nests, and combining this with field observations as done in our study,
184 is expected to result in overall high capture probabilities. Based on this, the use of the
185 number of trapped mice for calculating a proxy for density should be adequate even
186 without correcting for variation in capture probabilities. Seven trapping sessions were
187 known to have had very low sampling effort due to a lack of field assistants. To avoid
188 bias caused by this, we used an average of the number of individuals trapped at the
189 previous and next reliable trapping session to estimate density for these sessions. Low
190 variability in recapture rates when discounting these sessions of known low sampling
191 effort was later confirmed by the analyses (Supplementary material Appendix 2
192 Figure A3). The size of the study site varied between 1 and 10 hectares over the study
193 period (depending on the distribution of the sleeping nests and on sampling effort),
194 and we consequently estimated the size using a 100 % minimum convex polygon
195 (MCP) approach on the coordinates of the sampled nests at each trapping session. Our

196 resulting measure of the minimum number of adult mice present divided by the study
197 area represents a proxy for adult population density and not absolute population
198 density; nonetheless, we will refer to this measure as population density in the
199 remainder of this text. All three environmental variables were scaled and standardized
200 to allow for a comparison of their relative effects. We checked for multicollinearity
201 among environmental variables using Pearson correlations (Supplementary material
202 Appendix 1 Table A1). Data available from the Dryad Digital Repository: hyperlink
203 to be provided (Nater et al. 2016).
204
205 **Mark-recapture models**
206 We built multi-state mark recapture models (MSMR models, Lebreton et al. 2009) to
207 assess the effects of temperature, food availability and population density on female
208 survival and maturation rates, while accounting for temporally variable recapture
209 probabilities. Individuals were assigned to one of three different life stages: (1)
210 immatures representing offspring younger than four weeks of age, (2) philopatrics
211 which are offspring older than four weeks and which could have reached sexual
212 maturity, but did not show signs of reproductive activity yet, and (3) breeders which
213 showed signs of reproductive activity (perforate vagina or lactation) at least once
214 before in their life (Fig. 1). An individual can only be encountered in the immature
215 class once, as the trapping interval corresponds to 4 weeks. When an immature
216 survives to the next month with a survival probability S_i, it will have a probability ψ_{IP}
217 to become a philopatric and a probability ψ_{IB} (maturation rate) to become a breeder
218 directly if it becomes reproductively active at the same time. Philopatrics survive with
219 a probability S_p and have a maturation rate ψ_{PB} to become breeders, but may also be
220 re-encountered as philopatrics ($1 - \psi_{PB}$). Breeders survive with a probability S_b and

221 can only be re-encountered as breeders. They also represent the only stage able to
222 reproduce and therefore add new immatures to the population (R).
223 Our most general model included the recapture rates (p) as a function of life stage and
224 an interaction between year and season, to account for variation in sampling effort
225 over time. Survival (S) and maturation rates (ψ) were modelled as functions of life
226 stage, temperature, food availability and population density. The most general model
227 for survival included all possible two-way interactions, as well as three-way
228 interactions including life stage. The most general model for maturation on the other
229 hand included only interactions between environmental factors but not with stage. We
230 were unable to parameterize models with stage interactions due to data limitations. All
231 three models were estimated with a logit link function. The corresponding linear
232 predictors were thus transformed within their respective modelling framework using a
233 logit (survival, recapture) or multinomial logit (maturation) function to obtain the
234 actual rates.
235 We assessed the goodness of fit of our most general model by estimating the variance
236 inflation factor ĉ using the median ĉ approach implemented in program MARK. The
237 goodness of fit test indicated adequate fit of our global model to the data, with an
238 estimated median ĉ of 1.09. Therefore, it was not necessary to account for over
239 dispersion in our model selection (Anderson et al. 1994). Subsequently, we reduced
240 the most general model for model selection. Model selection was based on the Akaike
241 information criterion corrected for small sample size (AICc) (Burnham and Anderson,
242 2002). When alternative models were indistinguishable (ΔAICc<2), the model with
243 fewest parameters was retained. Our model selection procedure consisted of two
244 steps. (1) We first identified the best model for recapture rate (p), then proceeded with
245 the model optimization for maturation rates (ψ) and ultimately for survival rates (S).

(2) As the three models (p, ψ, S) are linked, we tested for potential effects of the order of model selection by comparing the best recapture rate model with reduced recapture rate models, while keeping the selected best models for survival and maturation. We proceeded likewise with the maturation rate model and finally the survival rate model.

Reproduction models

We modelled the probability of a breeder making a reproductive attempt (RA, indicated by perforate vagina or lactation) as a binomial generalized linear mixed model (GLMM). We considered temperature, food availability, and population density at the previous time-step (month) as fixed effects. Furthermore, we included individual identity and year as random effects on the intercept to account for individual and temporal heterogeneity generated by repeated measurements on the same individual and the same year.

Since individual-based data on the number of immature individuals added to the population (recruits) per mother and breeding event was not available, we used a population mean at each time-step t. We calculated this as the number of immatures trapped at time t divided by the number of active breeders trapped at time t-1. Additionally, we corrected both the number of immatures and the number of breeders by the recapture rates obtained from the MSMR model. Because these data contained many entries of 0, we used two different models to approximate the relationship between recruitment and temperature, food availability and population density at the previous time-step (month). We modelled the probability of any successful recruitment occurring (0 or 1) as a binomial GLM, and number of recruits per female (given that it is larger than 0) as another GLM with a gamma distribution. Parameters were estimated on the logit (probability of reproductive attempt, recruitment

probability) or log (recruit number) scale, and the corresponding linear predictors were transformed within the modelling framework using a logit or log function respectively. Model selection was based on AICc, as described before.

All analyses were run in R version 3.1.2 (R Core Team 2014). MSMR models were fitted using the RMark package (Laake 2013) which calls upon program MARK for model fitting (White and Burnham 1999). The median ĉ test was performed in program MARK directly. GLMMs were fitted using the lme4 package for R (Bates et al. 2015). We used built-in prediction functions where possible, and resorted to manual prediction of point estimates combined with the delta method (as described by Williams et al. 2001) and bootstrapping approaches for calculating confidence intervals where necessary.

Results

Survival

Our final model for survival rates included stage-specific effects of all three environmental covariates, as well as a two-way interaction between temperature and food availability and a three-way interaction between stage, food availability and population density (Supplementary material Appendix 4 Table A2). The estimates of monthly survival probability of immatures ranged from 0.50 to 0.98 (mean=0.80±0.13) over the study period. Philopatric survival varied between 0.55 and 0.98 with a mean of 0.83±0.08. Breeder survival had a mean of 0.81±0.05 and a range of 0.64 to 0.93. On average, our model predicted an association of high temperatures with higher survival of immatures (β=0.54, 95% CI [0.05, 1.04]) and philopatrics (β=0.25, 95% CI [0.09, 0.41]) but with lower survival of breeders (β=-0.11, 95% CI [-

296 0.22, 0.01], Fig. 2A). Increasing food availability was generally associated negatively
297 with survival of all life stages (average β=-0.09, Fig. 2B and 2C). There were
298 indications that the average effect of population density on survival was positive for
299 immatures (β=0.56, 95% CI [-0.03, 1.15]) and breeders (β=0.07, 95% CI [-0.03,
300 0.18]) but negative for philopatrics (β=-0.13, 95% CI [-0.27, 0.01], Fig. 2D). An
301 Interaction between temperature and food availability resulted in the model predicting
302 steeper declines in survival with increasing food availability if temperature was high
303 (Fig. 2A and 2B). The interaction between food availability and population density
304 was particularly strong and able to reverse the general pattern under high-density
305 conditions: for philopatrics and breeders, the negative relationship between survival
306 and food availability disappeared (Fig. 2C), and low food availability resulted in
307 philopatric and breeder survival decreasing (instead of increasing) as population
308 density became higher (Fig. 2D). Survival of immatures remained associated
309 negatively with food availability and positively with population density, irrespective
310 of variation in the other factor.
311
312 **Maturation**
313 Our final model for maturation rates contained single effects of stage, temperature,
314 food availability and population density as well as an interaction between temperature
315 and population density (Supplementary material Appendix 4 Table A3). The monthly
316 maturation rates estimated over the study period showed large variation and were
317 slightly higher for immatures (ψ_{IB}: 0.003 to 0.66, mean=0.18±0.16) than philopatrics
318 (ψ_{HB}: 0.003 to 0.63, mean=0.16±0.15). The selected model predicted that the
319 maturation rates of immatures and philopatrics decreased with higher temperature
320 (β=-0.94, 95% CI [-1.07, -0.81]), with lower food availability (β=0.43, 95% CI [0.32,

0.54]) and with higher population density (β=-0.41, 95% CI [-0.55, -0.28], Fig. 3). Furthermore, the negative impacts of population density and temperature amplified each other through an interaction (Supplementary material Appendix 3 Fig. A4). Another model ranking within 2AICc units of the most parsimonious one also provided support for an interaction between food availability and population density (Supplementary material Appendix 4 Table A3).

Recapture

Our final model for recapture rates included a single effect of life stage and an interaction between season and year (Supplementary material Appendix 4 Table A4). Recapture rates ranged from 0.30 to 0.95 for breeders (mean=0.84±0.12) and from 0.11 to 0.87 for philopatrics and immatures (mean=0.61±0.14) during the study period. Particularly high or low recapture rates were not associated with specific months. However, variation in recapture rates appeared to be larger before 2009, often coinciding with the few months of known low sampling effort, and average recapture rates have slightly increased between 2011 and 2015.

Reproductive attempts

Our final model for the probability of breeders making a reproductive attempt (RA) included single effects of all covariates as well as two-way interactions of temperature with food availability and temperature with population density (Supplementary material Appendix 4 Table A5). Monthly RA probabilities spanned a large range from 0.001 to 0.96. The mean RA probability was 0.43±0.30. The model predicted that RA probability became higher as temperatures decreased (β=-0.94, 95% CI [-1.11, -0.76], Fig. 4A and 4B), as food availability increased (β=0.82, 95% CI [0.58, 1.08], Fig. 4C)

346 and as population density decreased (β=-0.44, 95% CI [-0.62, -0.26], Fig. 4D).
347 Interactive effects resulted in RA probability at low temperatures being even higher if
348 food availability was high at the same time and if population density was low.
349
350 **Recruitment**
351 The probability of successful recruitment was explained best by a model containing
352 only the additive effects of food availability and population density (Supplementary
353 material Appendix 4 Table A6). The probability of successful recruitment ranged
354 from 0.08 to 0.97 (mean=0.45±0.26). The model predicted successful recruitment to
355 be more likely when food availability was high (β=1.22, 95% CI 0.72, 1.80]) and
356 population density was low (β=-0.52, 95% CI [-1.01, -0.07], Supplementary material
357 Appendix 3 Fig. A5).
358 Our selected model for the number of recruits per breeding female consisted of the
359 additive effects of temperature and population density (Supplementary material
360 Appendix 4 Table A7). The average number of recruits per female ranged from 0.16
361 to 1.25 (mean=0.44±0.23), and seemed to be larger under higher temperatures
362 (β=0.31, 95% CI [-0.05, 0.71]) and lower population density (β=-0.49, 95% CI [-0.99,
363 0.01], Supplementary material Appendix 3 Fig. A6). A second model containing an
364 additional positive effect of food availability explained variation in the data almost
365 equally well (Supplementary material Appendix 4 Table A7).
366

367 ## Discussion

368 In this study, we investigated the combined effects of exogenous and endogenous
369 factors on demographic rates of the African striped mouse. We found that
370 temperature, food availability and population density jointly affected demographic

371 rates, but that their impacts on specific rates varied considerably. Most importantly,
372 we demonstrated that interactions between exogenous and endogenous factors were
373 shaping environment-demography relationships. We found density-dependence in all
374 demographic rates, and these density effects were sometimes offset (e.g. in breeding
375 probability) or even reversed (e.g. in survival) by interactions with other
376 environmental factors. Considering these interactions allows for drawing further
377 inferences about the mechanisms underlying demographic variability and linking
378 them to previously reported seasonal patterns (Schradin and Pillay 2004; 2005).
379
380 **Survival**
381 Survival rates of all life stages were influenced considerably by temperature, food
382 availability and population density. Furthermore, we showed that interactions among
383 factors were crucial for understanding variability in survival rates. In accordance with
384 our first hypothesis, survival was positively associated with temperature for
385 immatures and philopatrics, indicating that higher costs of thermoregulation at low
386 ambient temperature decrease survival probability. Larger energetic costs arising from
387 hypothermia for earlier (hence smaller-bodied) life stages have previously been
388 shown in field voles (*Microtus agrestis*, Simons et al. 2011) and remain a likely
389 explanation of the observed pattern. For breeders, on the other hand, warmer
390 temperatures correlated with decreasing survival. This may be related to survival costs
391 of past reproduction and individuals dying of old age: temperature increases are
392 indicative of the onset of summer, and for breeders this will often coincide with the
393 end of the spring breeding season of their second year (Schradin and Pillay 2004).
394 Interactive effects of food availability resulted in more negative impacts of increasing
395 temperature, indicating that there may be additional survival costs associated with

high food availability. This becomes more apparent when the explicit relationships between survival and food availability are considered. We found survival of all life stages to be lower when food availability was high. This stands in stark contrast with our initial hypothesis and appears counter-intuitive, as high food availability has been associated with increased survival in, for example, leaf-eared mice (*Phyllotis darwinii*, Lima et al. 2001), which are ecologically very similar to striped mice. It is likely that unaccounted factors that decrease survival are associated with high food availability in this system. As outlined below, potential explanations for these unaccounted factors can be drawn when considering density effects in addition to and interacting with food availability.

Population density was correlated positively with survival of immatures, producing a pattern opposite to the negative relationship we had expected. For philopatrics and breeders, high population density had a negative impact on the survival under low-food conditions, as we had hypothesized. Under high-food conditions, however, the interaction between population density and food availability reversed the trend, making high population density beneficial to survival. Consequently, the relationship between density and survival of striped mice is consistent with two contrasting results from other rodents inhabiting semi-arid environments depending on the amount of food available: A negative density-survival relationship found for multimammate rats (*Mastomys natalensis*, Leirs et al. 1997) and a positive density-survival relationship found for leaf-eared mice (Lima et al. 2001, 2003).

Lima et al. (2003) argued that the latter could be due either to a predator saturation effect decreasing the chance of each individual to be killed, or to inhibition of dispersal resulting in higher apparent survival. Both explanations would be plausible mechanisms to explain the complex survival patterns arising from the interaction of

421 population density and food availability we observed for striped mice. As opposed to
422 other systems where high plant cover can provide rodents with shelter from predators
423 (Andreo et al. 2009, Schorr et al. 2009), high availability of annual food plants in the
424 Succulent Karoo can prompt striped mice to spend more time foraging in open areas
425 with little shrub cover (Schradin and Pillay 2006), exposing them to a higher risk of
426 predation. A predator saturation effect could then explain why the negative
427 association between food availability (= predation pressure) and survival disappears
428 under high population densities. Alternatively, the pattern could also be explained
429 through dispersal dynamics: when food availability is high (e.g. in the breeding
430 season) dispersal of female striped mice is negatively density-dependent (Schoepf and
431 Schradin 2012), and consequently increasing densities will result in reduced dispersal
432 and therefore higher apparent survival. During the non-breeding season (lower food
433 availability) female dispersal is density-independent and mostly absent (Schoepf and
434 Schradin 2012) and a different mechanism (e.g. competition) could then be
435 responsible for the negative density-survival relationship. Immature striped mice
436 apparently survived better when population densities were high irrespective of
437 interacting factors, potentially because they do not disperse, may be exempted from
438 strong resource competition with adults, and additionally benefit from increased
439 protection and alloparental care in larger groups (McGuire et al. 2002, Schradin
440 2013).
441 Our final survival model did not contain an interaction between population density
442 and temperature, even though we had hypothesized this to be important, as striped
443 mice can save energy by huddling in groups, which are larger when population
444 density is high. However, Scantlebury et al. (2006) found a reduction of energy
445 expenditure with increasing huddling group size only up to six individuals, a size that

446 can be reached at low to medium population densities. Energy saving due to huddling
447 is believed to be the main cause of group-living in striped mice (Schradin et al. 2012),
448 and striped mice may form groups of a minimum size to reach the maximal
449 thermoregulatory benefit independent of population density (Schradin et al. 2006).
450
451 **Reproduction**
452 Different demographic rates associated with reproduction (maturation rates, RA
453 probability, recruitment probability, recruit number) were affected by the studied
454 environmental factors in similar directions. Interactive effects on reproduction did
455 buffer the strength of environmental impacts slightly, but did not reverse any
456 environment-demography relationships as observed for survival.
457 The effects of temperature varied among different demographic rates related to
458 reproduction. Maturation rates and reproductive attempts were negatively related to
459 high temperatures, which could be a consequence of stress induced by hyperthermia,
460 low water availability and low food quality. Additional stressors in the form of
461 interacting low food availability and high population density exacerbated the negative
462 effect of increasing temperature, supporting the notion that overall poor
463 environmental conditions impair reproduction. For recruitment on the other hand, we
464 found indications of a positive relationship with temperature: the number of recruits
465 was slightly larger under higher mean temperatures. A similar trend was found by
466 Ferreira et al. (2006) for the house mouse (*Mus musculus*), and may relate to reduced
467 survival of offspring between birth and weaning due to hypothermia. Alternatively,
468 the positive association between recruitment and ambient temperature may be related
469 to maternal condition: breeding female striped mice increase in body mass and age
470 throughout the breeding season and therefore as temperature increases (Schradin pers.

observation) and litter size is known to be larger for older and heavier females (David and Jarvis 1985).

Our observations of positive associations between increased food availability and reproduction are in accordance with our initial hypothesis as well as numerous studies on other rodent species (e.g. Taitt 1981, Dobson and Oli 2001) including the previously mentioned ecologically similar leaf-eared mouse (Lima et al. 2001) and multimammate rat (Leirs et al. 1997). Our results thus support previous evidence that the availability of small annual plants is an important driver of rodent reproduction in semi-arid environments (Previtali et al. 2009), as such plants provide the amount of dietary water, vitamins (Beatley 1969) and especially protein (Nel et al. 2015) necessary to cover the physiological demands of reproduction. Furthermore, the relationship between reproduction and food availability was independent of temperature for all but one demographic rate, supporting the notion that striped mice are capable of opportunistic breeding at any time of the year if sufficient protein-rich food is available.

As predicted, all reproductive rates were negatively correlated with increasing population density. This result is intuitive, given that population density increases throughout the breeding season and peaks at its end. Concurrent with the increase in density in the course of the breeding season, the amount of protein found within food plants becomes less (because plants stop growing), resulting in gradual removal of the key physiological prerequisite of striped mouse reproduction (Nel et al. 2015). After the breeding season, the total availability of food plants and breeding territories decrease (Schradin et al. 2012), resulting in fewer resources per capita, and increasing competition, which could impair reproduction (Hestbeck 1982, Lima et al. 2001). This argument is further supported by our findings that maturation rate and probability of

making a reproductive attempt are unaffected by density at cool temperatures (beginning of the breeding season) when resources are abundant, plants are growing (high protein content) and competition might therefore be lower. In sum, the negative relationship between population density and reproduction might either indicate a direct negative impact of population density on reproduction, or simply indicate that population density is at its highest when reproduction ceases due to other factors.

Importance of interactions

Our study revealed the importance of considering interactions among environmental factors in the study of life-history variability and population processes. First, we reported strong interactive effects that both exacerbated or dampened demographic responses to environmental factors. These effects include, for example, how high temperature and low population density together resulted in even lower maturation rates, or how at lower temperatures the strength of the negative density feedback on the probability of reproductive attempts decreased, an interaction frequently reported in other rodent studies (e.g. Karels and Boonstra 2000, Previtali et al. 2010). Second, we also demonstrated that the strength of interactions may exceed simple modification of relationship strength (exacerbation or dampening) and affect even the general direction of environment-demography relationships. We showed this for the density feedback on survival in our study system, which is negative if food availability is low, and positive when food availability is high. Third, we demonstrated that the consideration of interactions has great potential for explaining contrasting environment-demography relationships between ecologically close-related species, such as the relationship between survival and population density outlined here for striped mice, leaf-eared mice and multimammate rats. Our comparison demonstrates

521 that studies may find apparently opposite environment-demography relationships in
522 similar species as a result of different and unaccounted levels of interacting covariates
523 instead of fundamental differences in the mechanistic processes underlying those
524 relationships. Our findings thus concur with recent studies (de Little et al. 2007,
525 Previtali et al. 2010, Griffiths et al. 2015) claiming that considering interactions is
526 crucial for gaining a detailed understanding of the roles of environmental drivers in
527 population regulation. Furthermore, considering the effects of interacting
528 environmental factors on demographic variability will allow building population
529 models including them as well. It will be important to investigate the role of
530 interactive environmental effects on outcomes and precision of population
531 projections, particularly under consideration of climate change. This constitutes a
532 promising venue for future research for the study system presented here, as well as
533 many others. While analytical tools for analysing demography and population
534 dynamics are becoming more and more flexible, the study of interactions remains
535 very data demanding, as illustrated by our analysis. Long-term individual-based data
536 with considerable temporal resolution is required to parameterize demographic
537 models including interactions. This highlights once more the great value and
538 importance of starting, maintaining and continuing long-term monitoring
539 programmes.
540

541 ## Conclusion

542 Demographic rates, and consequently population dynamics, change in response to
543 combinations of exogenous and endogenous environmental factors (Krebs 2013). In
544 this study, we found that not only the independent effects of temperature, food
545 availability and population density were important, but also that particularly

546 interactions between the different environmental factors were crucial for explaining
547 the observed demographic variability. As interactions affect population dynamics
548 non-additively and sometimes unexpectedly, identification of the underlying
549 mechanisms, for example using trait-based analysis (Coulson et al. 2001, Ozgul et al.
550 2010), is pivotal for forecasting species responses to environmental change (Griffiths
551 et al. 2015).
552

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Supplementary material (Appendix oik.XXXXX at <www.oikosjournal.org/readers/appendix>). Appendix 1-3

Figure 1. Life cycle of the African striped mouse. Survival probabilities are abbreviated as "S", maturation probabilities as "ψ" and reproduction as "R". The subscript denotes to which stage/transition a probability is specific (i=immature, p=philopatric, b=breeder, IP=immature to philopatric, IB=immature to breeder, PB=philopatric to breeder).

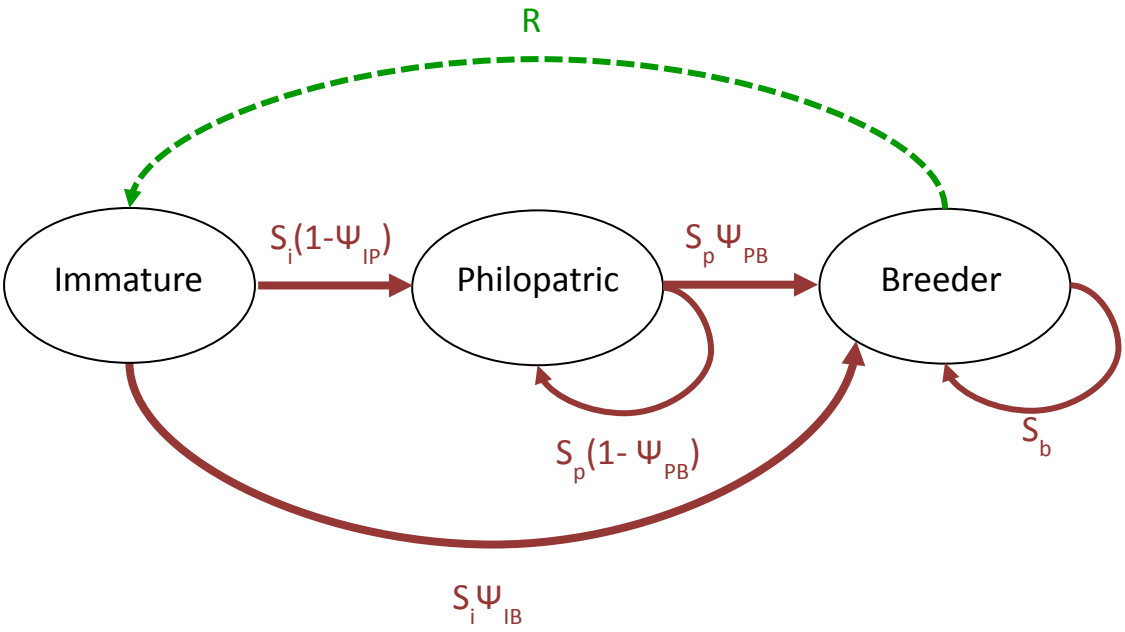

Figure 2. Model predictions for survival probability of immatures, philopatrics and breeders as functions of (A) temperature, (B) and (C) food availability and (D) population density. Solid lines represent point estimates predicted by the model; shaded areas are their 95% confidence intervals. The 3 panels in each row contain visualizations of the relationship at 3 different levels of one interacting covariate, from left to right: low (mean-sd), medium (mean) and high (mean+sd). All other covariates were set to the mean observed in the data.

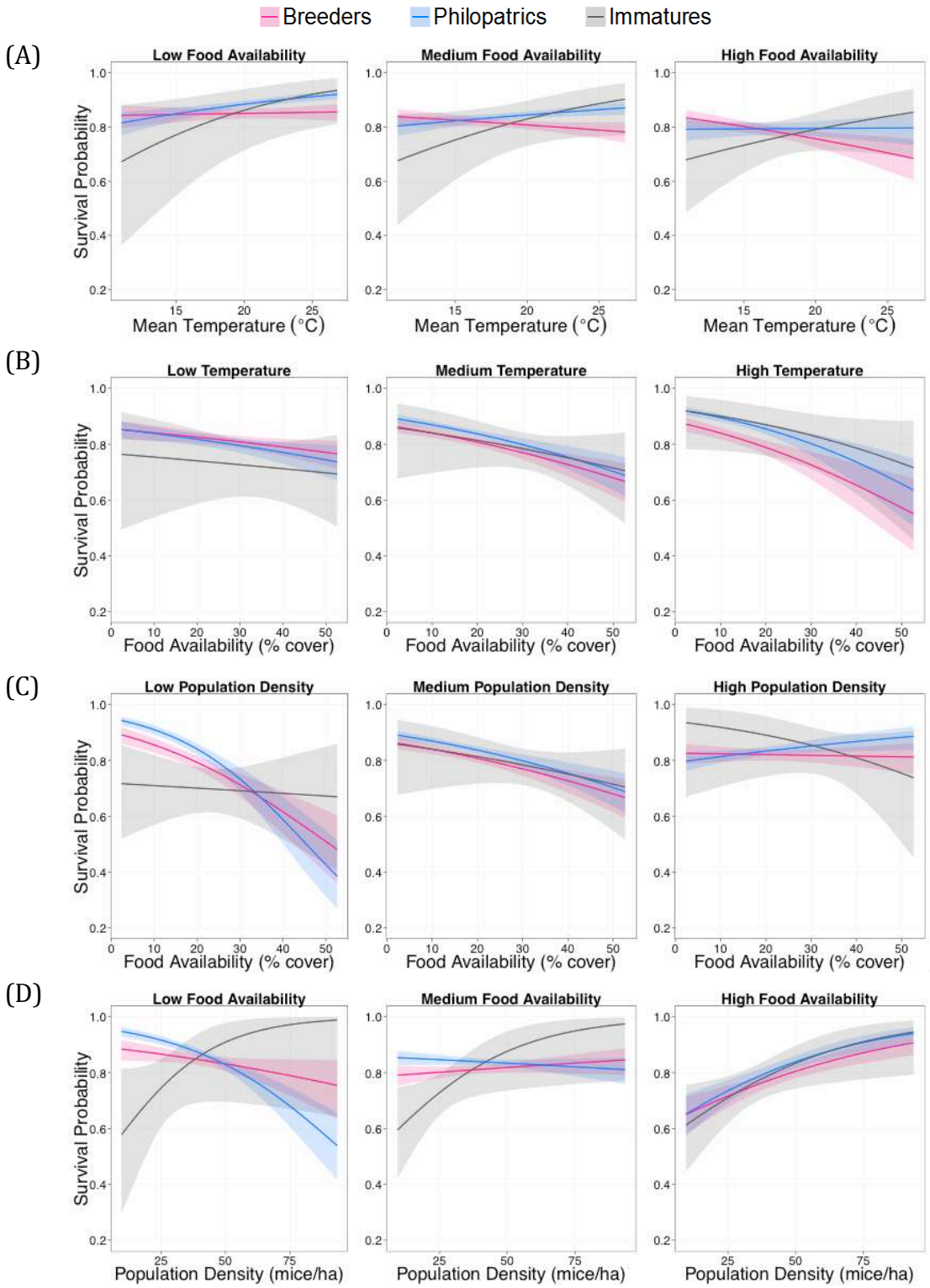

Figure 3. Model predictions for maturation rates of immatures and philopatrics as functions of temperature, food availability and population density. Solid lines represent point estimates predicted by the model; shaded areas are their 95% confidence intervals. All other covariates were set to the mean observed in the data.

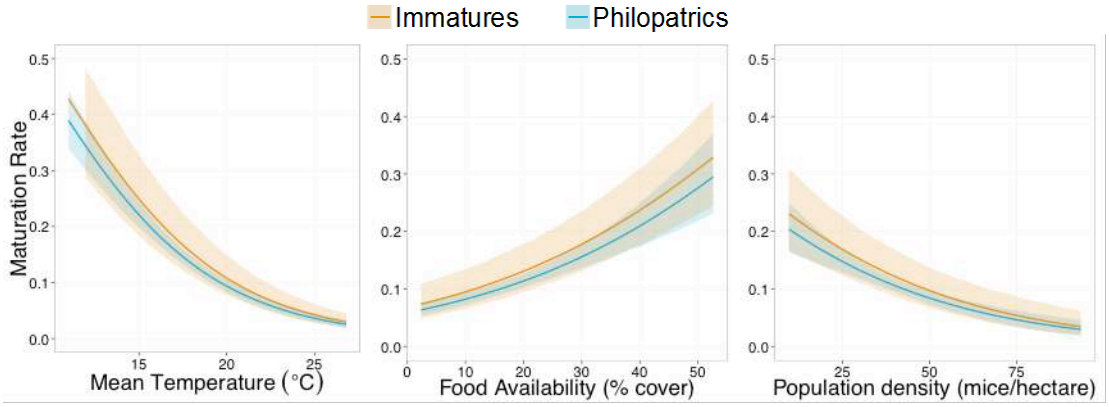

Figure 4. Model predictions for the probability of reproductive attempts of breeders as functions of (A) and (B) temperature, (C) food availability and (D) population density. Solid lines represent point estimates predicted by the model; shaded areas are their 95% confidence intervals. The 3 panels in each row contain visualizations of the relationship at 3 different levels of one interacting covariate, from left to right: low (mean-sd), medium (mean) and high (mean+sd). All other covariates were set to the mean observed in the data.

(A)

(B)

(C)

(D)